

## TAXONOMY OF THE GENUS APHANOSTEPHUS (Asteraceae-Astereae)

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### Abstract

Aphanostephus, a wholly North America genus largely confined to the southwestern United States and adjacent Mexico, is treated taxonomically. Four species are recognized: three annuals (A. skirrhobasis, with a chromosome number of  $2n=6$ ; A. ramosissimus, with  $2n=8$ ; and A. pilosus with  $2n=8$ ); and one perennial (A. riddellii, with  $2n=10$  or  $2n=20$ ). Aphanostephus skirrhobasis has three intergrading infraspecific taxa: var. skirrhobasis, var. thalassius and var. kidderi. The most widespread, variable, species, A. ramosissimus also includes three intergrading infraspecific taxa: var. ramosissimus, var. humilis and var. ramosus. Keys to the taxa and distributional maps are provided and a complete update on chromosome numbers is presented. The ancestral base chromosome number is believed to be  $x=5$  which perhaps gave rise to the lower numbers by descending aneuploidy.

The late L. H. Shinnars once confided to me that, of the several genera to come under his taxonomic scrutiny, the most difficult was Aphanostephus. This was so, he said, because the species are exceedingly plastic, both as to habit and head size (there being vernal and autumnal forms); in addition, he surmized that the various taxa tended to form hybrids so as to obscure specific boundaries.

This confession is attested to in Shinnars (1946) revision of the genus where he states, "Casual examination of an assortment of herbarium specimens assigned to several species may give the impression that an incoherent jumble has been divided at random into several equally incoherent jumbles, with no distinctions that hold good." Nevertheless, he did provide a very thorough, largely reliable, account of the genus for the United States, mostly by sorting sheets according to head size, foliage characteristics and habit. He was clearly not satisfied with his treatment of the Mexican material at his disposition, noting that "the untangling of the variations among the Mexican species has been fraught with much uncertainty, and has depended a great deal upon analogy with what is better known of the species in the United States." Indeed, some of the Mexican taxa recognized by Shinnars would be difficult, if not impossible, to distinguish from their more Northern counterparts, as will be noted below.

I became interested in Aphanostephus in 1954, shortly after my

arrival at the University of Texas, largely because several of the species are among the more abundant roadside weeds of Central Texas and because preliminary examination showed them to possess very low chromosome numbers ( $2n=6, 8$  or  $10$ ).

I worked on the genus for several years, but unlike Shinnors, I soon found the Texas species to be relatively easily recognized, both in the field and in the herbarium. This was largely due to my use of chromosomal and micromorphic features, characters which Shinnors largely, if not entirely, ignored. Indeed, what appeared upon superficial examination to be "incoherent jumbles" were soon resolved into coherent assemblages. In fact, I was never able to discern a single instance of interspecific hybridization, even when three or more species of Aphanostephus were found cohabiting the same general area (e.g., within several hundred meters of each other, or sometimes growing intermixed, as often occurs with populations of A. skirrhobasis and A. ramosissimus).

The taxonomic simplicity of the group was neatly revealed by chromosomal studies in which the largely, more eastern species of sandy soils, Aphanostephus skirrhobasis, was found to be consistently diploid with  $2n=6$  chromosomes; the largely more western species of silty-clay, drier soils, A. ramosissimus, was found to be consistently diploid with  $2n=8$  chromosomes; while the widespread, but less common species of shallow calcareous soils, A. riddellii, was found to be diploid or tetraploid with  $2n=10$  or  $2n=20$  chromosomes. Further, it soon became clear as a result of much field work that the eastern A. ramosissimus ( $2n=8$ ) graded into a more robust, larger headed western phase which Shinnors (following A. Gray) recognized as A. arizonicus. Field work in southern Texas also revealed that A. skirrhobasis ( $2n=6$ ) graded into what Shinnors took to be a very distinct taxon, A. kidderi ( $2n=6$ ).

Ignoring the very distinct, relatively localized species, Aphanostephus pilosus with  $2n=8$ ,  $F_1$  hybrids between the widespread, often sympatric, species mentioned above should be readily recognized since each has different chromosome numbers. In the numerous sites where I have found two (or sometimes three) of these species growing together, and in which I thought I detected putative hybrids (as detected by head size, habit and habitat), examination of meiotic chromosomes proved me wrong: such "hybrids" were invariably normal-pairing diploids with  $2n=3, 4$  or  $5$  chromosomal pairs.

In the process of examining these various meiotic squashes a simple observation became apparent: one could predict the chromosome number of any given collection by the kinds of hairs borne upon the minute ovaries. If on the ovaries why not the mature achene? Ah yes, there too! If Shinnors had examined the achenes at whatever stage of development he could have readily identified all of the specimens to species by their hairs alone.

The achenal hairs of *Aphanostephus* are comprised of two tiers of cells, as is usual for most taxa of the Astereae. In the three taxa concerned the achenal hairs assume three forms: straight hairs in *A. ramosissimus* ( $\bar{x}=4$ ); coiled hairs in *A. skirrhobasis* ( $\bar{x}=3$ ); and barbed hairs in *A. riddellii* ( $\bar{x}=5$ ). This is readily seen under magnifications of  $\times 30$  in a good stereomicroscope and may be sketched as follows:

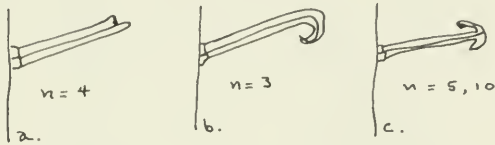


Fig. 1. Achenal hairs in *Aphanostephus* as correlated with chromosome numbers.

Thus it was that the *Aphanostephus* "complex" within the confines of the United States became a fairly comprehensible group; there are four well-defined specific taxa as follows:

1. *A. pilosus* - a quite distinctive species with  $\bar{n}=4$  pairs; endemic to north-central Texas and adjacent Oklahoma.
2. *A. skirrhobasis* -  $\bar{n}=3$  pairs; widespread weedy species of mostly central and eastern Texas but readily adventive elsewhere. This includes *A. kidderi*.
3. *A. ramosissimus* -  $\bar{n}=4$  pairs; widespread weedy species of more western regions, principally in calcareous or mixed calcareous soils. This includes *A. arizonicus* and most of the Mexican populations.
4. *A. riddellii* -  $\bar{n}=5$  or 10 pairs; widespread but infrequent perennial species of rocky or shallow, well-drained calcareous soils.

After several years work, then, I was content that the species of the United States posed no great taxonomic problems and that Shinnery's treatment, except as to the nomenclatural rank accorded the intergrading taxa (*A. arizonicus* and *A. kidderi*, mentioned above), was basically sound.

Nevertheless, it was clear that the Mexican material was poorly known, much as Shinnery indicated, and attempts to identify plants from this region using Shinnery's "Outline of the Mexican Species" proved unreliable, inconsistent and at odds with what seemed to be good biological judgment (i.e., some of the Mexican taxa seemed morphological indistinguishable from Texas taxa). No doubt much of

this inadequacy was occasioned by the limited material available to Shinnery, to say nothing of his unfamiliarity with their populational variability in the field.

After working out what seemed to be a sound biological treatment, I felt that the genus might be an expedient taxon for detailed biosystematic study, especially if one were willing to undertake synthetic crosses so as to ascertain if the aneuploidy detected in the group was descending or ascending. To this end I assigned the genus to Mr. Arnold Birdsong for a doctoral problem, hoping that his studies might ultimately resolve the populational problems in Mexico. He worked on the genus for several years but never put together a treatment of the group and ultimately opted to pursue a career in the Medical Sciences. I am pleased to note that he now has his M.D. and is practicing his profession.

Before abandoning his project Mr. Birdsong personally annotated several thousand sheets from numerous herbaria but, unfortunately, he never prepared a formal draft of his views on the relationships of the various taxa. Because of this I have felt some compulsion to provide at least an overview of both his work and my own. In this I hope my taxonomic views are not radically different from those which Arnold might have come to. Whatever the case, I take full responsibility for the interpretations rendered and the nomenclature accorded.

Because of the careful and thorough descriptions of the genus and subordinate taxa rendered by Shinnery (1946) these are not reiterated here. His treatment of the Mexican taxa, as noted, was based upon very limited material and no field work. Recent collections and much field observation has led me to believe that all of the Mexican material, except for A. riddelli and A. skirrhobasis, belong to but a single widespread, variable species, A. ramosissimus. Thus all of the Mexican names proposed for the latter by Gray (A. arizonicus, A. humilis and A. ramosus) and those proposed by Shinnery (A. potosinus and A. jaliscensis) are either treated as but regional intergrading populations deserving of varietal rank only, or else reduced to synonymy among these infraspecific taxa.

#### Chromosome Counts

Jackson (1957) published the first chromosome number for Aphanostephus, reporting  $n=4$  pairs for A. arizonicus (= A. ramosissimus var. humilis). Since that time 100 or more chromosome counts have been reported for the genus (Table 1), including reports for all of the described taxa. Most of these have been made by the present author or by Dr. Arnold Birdsong, beginning about 1957, and have largely gone unreported.



Table 1. Chromosome numbers in *Aphanostephus*.

<u>Species</u>	<u>Voucher* or Reference</u>	<u>2n - number (prs.)</u>
<u>A. riddellii</u>	Texas. Bexar Co.: Turner 4546; 4548B.	5 II
	Texas. Coke Co.: Raven 19280.	5 II
	Texas. Glasscock Co.: Turner 4955.	5 II
	Texas. Travis Co.: Turner 4421.	5 II
	Texas. Uvalde Co.: Turner 5009.	5 II
	Texas. Val Verde Co.: Thompson 210.	5 II
	Texas. Val Verde Co.: Tomb 216.	5 II
	Mexico. Coahuila: Powell & Powell (1978).	5 II
	<u>A. pilosus</u>	Turner and Crammer (1964).
<u>A. ramosissimus</u> var. <u>ramosissimus</u>	Oklahoma. Woodward Co.: Keil 10738.	4 II <sup>C</sup>
	Texas. Bee Co.: Turner 4464.	4 II
	Texas. Bexar Co.: Turner 4396; 4548A.	4 II
	Texas. Dimmit Co.: Turner 4998.	4 II
	Texas. Frio Co.: Turner 4992.	4 II
	Texas. Hidalgo Co.: Turner 4483.	4 II
	Texas. Jim Wells Co.: Thompson 179	4 II
	Texas. Kent Co.: Turner 4709.	4 II
	Texas. Hardemon Co.: Flyr 1319.	4 II
	Texas. Menard Co.: Raven 19261	4 II <sup>a</sup>
	Texas. Real Co.: Turner 38.	4 II
	Texas. Starr Co.: Turner 4500; 4511.	4 II
	Texas. Terrell Co.: Raven 19197.	4 II <sup>a</sup>
	Texas. Travis Co.: Turner 4428.	4 II
	Texas. Uvalde Co.: Turner 4427.	4 II
	Texas. Webb Co.: Turner 4510.	4 II
	Mexico. Tamaulipas: Whalen 274.	4 II
<u>A. ramosissimus</u> var. <u>humilis</u>	Ariz. Darlington (1957).	4 II
	Ariz. Pima Co.: Raven et al. (1960).	4 II (2n=8)
	N. Mex. Bernalillo Co.: Jackson (1960).	4 II
	N. Mex. Dona Ana Co.: Turner 5749.	4 II
	N. Mex. Lincoln Co.: Raven 19139.	4 II <sup>a</sup>
	N. Mex. Socorro Co.: Keil 10738.	4 II <sup>C</sup>

	Texas. El Paso Co.: <u>Turner 6138.</u>	4 II (2n=8)
	Mexico. Chihuahua: DeJong & Longpre (1963).	4 II
	Mexico. Chihuahua: Keil 8263A.	4 II <sup>d</sup>
	Mexico. Chihuahua: <u>Powell &amp; Powell (1978).</u>	4 II
	Mexico. Chihuahua: <u>Stuessy 1097.</u>	4 II
	Mexico. Chihuahua: <u>Sikes 404.</u>	4 II
	Mexico. Durango: <u>King 3752.</u>	4 II
	Mexico. Durango: <u>DeJong &amp; Longpre (1963).</u>	4 II
	Mexico. Nuevo Leon: <u>Rock M-272.</u>	4 II
	Mexico. Nuevo Leon: <u>Johnston 4204B.</u>	4 II
	Mexico. San Luis Potosi: <u>Breedlove 14355.</u>	4 II <sup>b</sup>
<u>A. ramosissimus</u>	Mexico. Hidalgo: <u>Powell 1112.</u>	4 II
var. <u>ramosus</u>	Mexico. Hidalgo: <u>Johnston 4760.</u>	4 II
	Mexico. Michoacan: <u>DeJong D758.</u>	4 II
	Mexico. Michoacan: <u>King 3606.</u>	4 II
	Mexico. Michoacan: <u>Powell 815.</u>	4 II
	Mexico. Michoacan: <u>Strother 1079.</u>	4 II
	Mexico. Puebla: <u>Beaman 3614; 3621</u>	4 II
	Mexico. Puebla: <u>Powell 633.</u>	4 II
<u>A. skirrhobasis</u>	Texas. Frio Co.: <u>Turner 4565;</u>	3 II
var. <u>kidderi</u>	4986; 4991.	
	Texas. Zavala Co.: <u>Sullivan 20;</u>	3 II
	21.	
	Texas. Zavala Co.: <u>Turner 5004.</u>	3 II
<u>A. skirrhobasis</u>	Oklahoma. Blaine C.: <u>Tomb 155.</u>	3 II
var. <u>skirrhobasis</u>	Oklahoma. Harmon Co.: <u>Flyr 1318.</u>	3 II
	Oklahoma. Pontotoc Co.: <u>Tomb 157A,</u>	3 II
	B.	
	Oklahoma. Woodward Co.: <u>Keil 10891.</u>	3 II <sup>c</sup>
	Texas. Atascosa Co.: <u>Turner 4554.</u>	3 II
	Texas. Bastrop Co.: <u>Brown 6106.</u>	3 II
	Texas. Burnett Co.: <u>Semple (1980).</u>	3 II
	Texas. Burnett Co.: <u>Turner 4420.</u>	3 II
	Texas. Caldwell Co.: <u>Thompson 26.</u>	3 II
	Texas. Coke Co.: <u>Raven 19282.</u>	3 II <sup>a</sup>
	Texas. Colorado Co.: <u>Thompson 88.</u>	3 II
	Texas. Ector Co.: <u>Tomb 140.</u>	3 II
	Texas. Frio Co.: <u>Irwin 1398.</u>	3 II
	Texas. Gonzales Co.: <u>Thompson 23;</u>	3 II
	86.	
	Texas. Jim Hogg Co.: <u>Thompson 178.</u>	3 II
	Texas. Kleberg Co.: <u>Turner 4318.</u>	3 II

	Texas. Llano Co.: <u>Turner 4391</u> ;	3 II
	<u>4392</u> ; <u>4393</u> .	
	Texas. Mitchell Co.: <u>Raven 19285</u> .	3 II <sup>a</sup>
	Texas. Palo Pinto Co.: <u>Turner 5042</u> .	3 II
	Texas. Wharton Co.: <u>Smith and</u>	3 II <sup>e</sup>
	<u>Johnson (1964)</u> .	
	Texas. Wilson Co.: <u>Turner 4422</u> .	3 II
<u>A. skirrhobasis</u>	Texas. Galveston Co.: <u>Turner 4415</u> ;	3 II
var.	<u>4418</u> .	
<u>thalassius</u>	Texas. Galveston Co.: <u>Raven 19419</u> .	3 II <sup>a</sup>
	Texas. Galveston Co.: <u>Semple (1980)</u> .	3 II

<sup>a</sup>Data from Solbrig et al. (1969).

<sup>b</sup>Data from Anderson et al. (1974).

<sup>c</sup>Data from Keil and Pinkava (1976).

<sup>d</sup>Data from Keil & Stuessy (1975).

<sup>e</sup>Plus 4 microchromosomes.

\*On file at TEX.

It is clear that Aphanostephus is mostly diploid with  $\bar{n}$  numbers of 5, 4 and 3. Fedorov (1969) lists a count of  $\bar{n}=7$  for A. skirrhobasis, crediting this to Smith and Johnson (1964), but the latter authors clearly note the count concerned to be  $\bar{n}=3$ , there being 4 additional, dividing, chromatin bodies which they describe as "microchromosomes". We never observed such bodies in our own numerous meiotic preparations of this taxon, although occasional accessory or B-type chromosomes were noted.

The only tetraploid counts found to date have been those for A. riddellii, which is largely diploid with  $\bar{n}=5$  pairs, but occasional populations from southcentral Texas are tetraploid with  $\bar{n}=10$  pairs.

Whether the numbers represent a descending series from a base chromosome number of  $\bar{x}=5$  or an ascending series on a base of  $\bar{x}=3$  is anybody's guess. Smith and Johnson (1964) thought that  $\bar{n}=3$  was derived from a taxon with  $\bar{n}=4$ , and it might be that the latter number gave rise to both  $\bar{n}=3$  and  $\bar{n}=5$  by descending and ascending aneuploidy respectively. It should prove meaningful to obtain crosses between these several chromosomal groups, but all attempts to obtain such combinations failed (perhaps this aspect of the study was not pursued with enough vigor by the present author, but it seems notable that hybrids were never found in nature, even when the several taxa concerned grew in close proximity).

One thing does seem clear, however: the ancestral base chromosome number for Aphanostephus was probably not  $\bar{x}=9$ , as might be championed by earlier workers on the tribe Astereae (Solbrig, 1977). The genus is not easily related to any North American member of the Astereae, what with its conical receptacles, columnar achenes and sometimes paleaceous pappus. Superficially the species of Aphanostephus look like Erigerons or Asters but the genus is so different in its floral and fruit characters as to suggest a very remote relationship with these two genera.

#### Generic Relationships

Shinners (1946) relates the genus to Dichaetophora ( $\bar{x}=3$ ) and Astranthium ( $\bar{x}=4$ ); he is probably correct in this assumption. These two genera, however, are themselves quite remote from Aphanostephus, to judge from their floral and fruiting structures, which strengthens my belief that these several chromosomal lines are ancestral relicts from some low base chromosome number for the tribe Astereae as a whole, either  $\bar{x}=4$  or 5, much as I have (Turner, 1977) postulated for Heterotheca ( $\bar{x}=5, 4$  and 9, sensu lato), Aster ( $\bar{x}=5, 8$  and 9) and Machaeranthera ( $\bar{x}=5, 4$  and 9), relatively remote genera, all belonging to the tribe Astereae. And if one wishes to consider the large genus Haplopappus, as treated by Hall (1928), to be a monophyletic assemblage, one cannot help but note that Hall himself considered the section Osbertia to be the primitive element within

Haplopappus, and that too has a base number of  $\underline{x}=5$  or 4 (Turner, unpubl.).

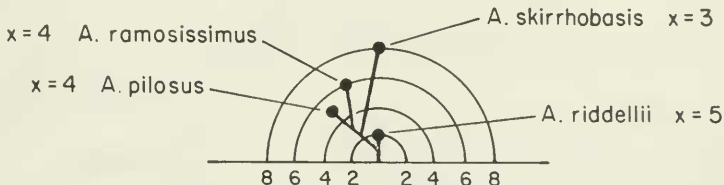
That Aphanostephus is a relatively unspecialized, indeed remote, member of the tribe Astereae may be inferred from Bentham's remark (1873, p. 409) that Bellis itself (the genus to which he relates Aphanostephus) "may be said to approach some Anthemideae in the Old World, and in the New World, through Aphanostephus, to pass into Egletes and the more tropical Grangea type". Bentham goes on to emphasize that the Grangea group links the tribe Astereae with the tribe Anthemideae, this based primarily on achenal structure, most of the taxa possessing non-flattened achenes, much as does Aphanostephus.

Bentham's conjecture that Aphanostephus or, indeed, Grangea might link the tribe Astereae to the Anthemideae, is not borne out by palynological studies, for both Aphanostephus and Grangea have pollen typical of the tribe Astereae while that of the tribe Anthemideae is radically different (Turner, 1977).

### Species Relationships

Blake (1937) recognized two subgenera under Aphanostephus: subgen. Pappophanus containing those taxa with a pappus of scales (A. pilosus, A. skirrhobasis and A. kidderi); and subgen. Aphanostephus containing A. ramosissimus, A. riddellii, and related taxa with a pappus of minute cilia. Shinnars, however, reduced both subgenera to sectional rank, using the name Pappopocus for the subgenus Aphanostephus, contrary to the present Code.

Unlike Blake or Shinnars, I can see little need, to recognize infrageneric categories for the relatively few taxa concerned. As noted below, A. skirrhobasis ( $\underline{n}=3$ ) was probably derived from a species with  $\underline{n}=4$ , presumably a taxon ancestral to both A. pilosus and A. ramosissimus as noted in the following:



The hypothetical phyletic relationships shown above assumes that the perennial Aphanostephus riddellii, with a base chromosome number of  $\underline{x}=5$ , has retained more primitive features than has the other species. Primitive vs advanced features are judged as follows:

primitive (0)	advanced (1)	very advanced (2)
1. chromosome base, x=5	x=4	x=3
2. habit perennial	annual	—
3. disk corolla-tube not inflated	inflated and indurate	—
4. achenal hairs straight	coiled or barbed	—
5. pappus of scales	pappus of cilia	pappus of indurate crown or fused scales
6. ray florets numerous (50+)	ray florets 8-34	—

By assigning values of 0, 1 and 2 to each of the above states it can be surmized that A. riddellii with a numerical value 2 is less advanced than the other species, while A. pilosus, A. ramosissimus and A. skirrhobasis are more advanced, possessing scores of 6, 5-6 and 7-9 respectively, depending upon the variety under consideration.

Of course this tabulation is highly biased. Other characters could have been chosen for such polarizations but I would have had little confidence in their validity. Those few chosen seem adequate and better than none. More rigorous cladistic analysis would have been preferred but, as noted above, it is difficult to find an out-group against which to assess the characters, Aphanostephus seemingly being a transitory genus between this or that. In short, out-group selection, depending upon the choice, would, in this instance, prove more whimsical for systematic purposes than the simplistic approach selected here.

#### TAXONOMIC TREATMENT

##### Key to Species of Aphanostephus

1. Hairs on achene coiled (Fig. 1a); pappus uneven and scaly or rarely composed of 5-10 acute to awn-tipped scales, 0.2-2.0 mm long; chromosome numbers,  $2n=6$  -----3. A. skirrhobasis

1. Hairs on achene straight or very minute and each cell abruptly reflexed near apex forming a prong-shaped structure; pappus a ring of very short, nearly equal, cilia, 0.1-0.25 mm long; chromosome numbers,  $2n=8, 10$  or  $20$ .

2. Achenal hairs minute, pronged (Fig. 1c.); perennials; chromosome numbers  $2n=10$  or  $20$ -----4. A. riddellii

2. Achenal hairs straight, not minute and pronged



(Fig. 1b); annuals; chromosome numbers  $2n=8$ .

3. Plant coarsely hispid with jointed, translucent hairs, those of the stem 0.6-2.4 mm long, spreading at right angles; ray florets 13-21; north-central Texas and adjacent Oklahoma-----2. A. pilosus

3. Plant softly pubescent, the hairs mostly adpressed, 0.2-0.8 mm long; rays 34 or more (except rarely on depauperate or autumnal forms); widespread species-----1. A. ramosissimus

1. APHANOSTEPHUS RAMOSISSIMUS DC., Prod. 5:310. 1836.

The following intergrading varieties are recognized and each are discussed in more detail below:

1. Involucres 3.2-4.8 mm high; pappus a cupuliform or raised crown, 0.15-0.30 mm high; achenes 1.2-1.4 mm long; plants of northeastern Mexico (eastern Coahuila, northern Nuevo Leon and Tamaulipas) and adjacent United States-----1a. var. ramosissimus

1. Involucres 4.7-7.5 mm high; pappus crown absent or nearly so; achenes 1.4-1.6 mm long; plants of southwestern United States and northcentral Mexico southward to Mexico City area [2].

2. Upper leaves mostly not clasping; stems usually erect, arising from a lignescent, usually unswollen, tap-root; plants from highland plateau regions of central Mexico (Guajuato-San Luis Potosi) northward to southwestern United States-----1b. var. humilis

2. Upper leaves mostly clasping; stems usually prostrate or recumbent, arising from a swollen tap-root; plants of trans-volcanic montane regions of south-central Mexico (Veracruz-Guerrero)-----1c. var. ramosus

1a. A. RAMOSISSIMUS DC. var. RAMOSISSIMUS

My interpretation of this taxon is essentially the same as Shinnars' (1946). The type, as noted by him, was collected by Berlandier, presumably near San Antonio, Texas in Bexar County. Shinnars thought that this taxon hybridized with A. skirrhobasis but, as noted above, hybridization between these taxa was never observed by the present author. Shinnars also suggested that A. ramosissimus might hybridize with "A. arizonicus"; I treat the

latter taxon as a regional variety of the present species (var. humilis, cf. below) and emphasize the fact that intergrades between these taxa can be found across a broad front in northcentral Mexico and western Texas (Fig. 2). This intergradation is gradual and does not appear to be due to in situ gene exchange between distinct entities.

Aphanostephus potosinus (type from Minas de San Rafael, San Luis Potosí, Mexico) is said to possess a combination of quantitative characters which serve to distinguish this from both A. arizonicus and A. humilis but I find nothing of substance to justify specific recognition. The several plants cited by Shinnars are mostly from central and southeastern San Luis Potosí and appear to be subtle regional intergradants between var. humilis, var. ramosissimus and var. ramosus, these several taxa converging, geographically, in this area (Fig. 2).

1b. APHANOSTEPHUS RAMOSISSIMUS DC. var. HUMILIS (Benth.) Turner and Birdsong, *Phytologia* 45: 501. 1980.

Aphanostephus humilis (Benth.) A. Gray, 1880.

Aphanostephus arizonicus A. Gray, 1880.

Aphanostephus potosinus Shinnars, 1946.

[See Shinnars, 1946, for additional synonymy.]

Shinnars treated Aphanostephus humilis (type from Guanajuato, Leon, Mexico) as distinct from A. arizonicus (type from Gila Valley, Arizona, U.S.A.) noting that the latter "has generally passed" as the former. He constructed a tedious and difficult key to distinguish between these but the only definitive "character" appears to be that of geography; that is, plants of northern Mexico and adjacent U.S.A. belong to A. arizonicus and those of central Mexico belong to A. humilis. The large suite of specimens from northern Mexico which I examined show nothing in the way of character states to justify varietal status, much less specific status.

Shinnars also speaks of "intermediates" between Aphanostephus skirrhobasis and A. ramosissimus which "are difficult to distinguish from A. arizonicus" but, as noted above, natural hybridization between these very distinct taxa probably does not occur and it is doubtful that any  $F_1$  hybrids would take on the characters of Shinnars' A. arizonicus.

1c. APHANOSTEPHUS RAMOSISSIMUS var. RAMOSUS (DC.) Turner and Birdsong, *Phytologia* 45: 501. 1980.

Aphanostephus ramosus (DC.) A. Gray, 1880.

Type from Michoacan.

Aphanostephus jaliscensis Shinnars, 1946. Type from Jalisco.

Aphanostephus pachyrrhizus Shinnery, 1946. Type from Puebla.  
[See Shinnery, 1946, for additional synonymy.]

This taxon forms fairly uniform populations in the volcanic highlands of southcentral Mexico, especially in disturbed ashy soils from 2000-3000 meters. Plants are characteristically prostrate or procumbent, possess mostly clasping upper leaves and have swollen, annual or biennial (?), tap roots. I have, however, observed considerable variation in these characters under field conditions, suggesting that their expression is under relatively weak genetic control. In any case, intergrades between var. ramosus and var. humilis occur northward and, probably, were names not already available for each of these, I might have recognized but a single taxon, so much alike they are in floral and fruit characters.

2. APHANOSTEPHUS PILOSUS Buckley

My interpretation of this species is the same as Shinnery (1946).

3. APHANOSTEPHUS SKIRRHOBASIS (DC.) Trel., 1891.

My interpretation of this species is essentially the same as Shinnery (1946) except that I would recognize 3 intergrading regional infraspecific taxa (reducing his A. kidderi to varietal status) instead of two, as follows:

1. Plants low, bushy and much-branched from the base; leaves thickened and densely, almost felty, gray-pubescent; plants of active or stable sand dunes along the GulfCoastalRegions-----lb. var. thalassius

1. Plants erect, usually sparsely-branch below; leaves not particularly thickened and not almost felty gray-pubescent beneath; interior populations on sandy soils.

2. Pappus of 5 or 10 acute or awn-tipped scales, mostly 0.4-2.0 mm long; plants of southcentral Texas and adjacent Mexico-----lc. var. kidderi

2. Pappus an uneven, often awn-tipped, or ciliate scaly crown mostly 0.2-1.8 mm long; widespread taxon-----la. var. skirrhobasis

3a. APHANOSTEPHUS SKIRRHOBASIS (DC.) Trel. var. SKIRRHOBASIS  
Synonymy as listed by Shinnery (1946).

Shinnery thought that "certain puzzling variations" of this taxon were due to interspecific hybridization but, as I have noted above, this is unlikely. My own field experience over a 30 year period with numerous populations leads me to believe that the

variety is exceptionally plastic with respect to habit, leaf shape and head size. Since these were the primary characters employed by Shinnars, along with pappus size (also very variable), it is not surprising that perplexing plants might be found. Shinnars also described two new forma, f. quasigigantiusculus and f. incisifolius, the former a depauperate form of typical var. skirrhobasis, the latter a leaf form.

This variety intergrades with var. thalassius over a broad region along the Gulf Coast and in such areas populations vary within and among themselves with regard to the characters used to distinguish between these. The same is true for the var. kidderi, but intergrades between the latter occur in a more localized region.

3b. APHANOSTEPHUS SKIRRHOBASIS var. THALASSIUS Shinnars, Wrightia 1: 106. 1946. TYPE. TEXAS: Galveston Co.: seashore S of High Island, 15 May 1945, L. H. Shinnars 7718 (holotype SMU).

My evaluation of this taxon is essentially the same as Shinnars. He notes that occasional plants of var. skirrhobasis are hard to separate from var. thalassius, "but the latter shows such uniformity and is so characteristic in appearance that it deserves nomenclatorial (sic) recognition." I ascribe to this view but believe that the intergradation, especially in southern Texas, is much more apparent than he suggested.

As indicated in Fig. 4, var. thalassius occurs on stabilized and active dune sands along the Gulf Coastal Regions from northeastern Mexico to Louisiana. The disjunct populations in Florida (cited by Shinnars, 1946) also occur in dune sand and perhaps represent relatively recent introductions (i.e., over the last 100 years or so).

Shinnars cites but a single collection from Mexico (Runyon 442, C, US) where it occurs on dune sand south of Matamoras, Tamaulipas. No doubt additional sorties along the coastal dunes of northeastern Mexico will reveal its presence elsewhere in this poorly collected region.

3c. APHANOSTEPHUS SKIRRHOBASIS var. KIDDERI (Blake) B. L. Turner, comb. nov. - Based upon Aphanostephus kidderi Blake, Contr. Gray Herb. 53: 23. 1918.

My interpretation of this taxon is about the same as Shinnars except that I do not ascribe to his view that "it apparently hybridizes" with Aphanostephus ramosissimus, although the two often grow together.

Shinnars also does not mention the obvious intergradation of var. skirrhobasis with var. kidderi in southcentral Texas as noted

in my Fig. 5 . Careful collection of several populations across a small region in this area revealed populational intergradation, some plants in any one populational referable to one taxon or the other. Away from the region of intergradation the diagnostic characters become stabilized. I take this to be regional intergradation due to primary divergence, and not that of secondary intergradation where allopatric hybridization is a factor (cf. Flake, Turner and Urbatsch, 1978).

Shinners cited a number of collections of this taxon, all from Texas. I would like to place on record the following collections from MEXICO: Tamaulipas: 2 km SW Nuevo Laredo, Dominguez & McCart 8297 (TEX); 24 km S Nuevo Laredo, Dominguez & McCart 8222 (TEX); 18 mi S Nuevo Laredo, Escalante 43 (TEX); 1 mi E Nuevo Laredo, Ibarra 112 (TEX); 12 mi S Nuevo Laredo, Saenz 55 (TEX).

4. APHANOSTEPHUS RIDDELLII T. & G. 1842.  
A. perennis W. & S., 1913.

My interpretation of this species is the same as Shinners. He rightly notes that it is easily recognized, often grows with the other species of Aphanostephus and does not form intermediates with these.

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Fig. 2. Distribution of varieties of *A. ramosissimus*.

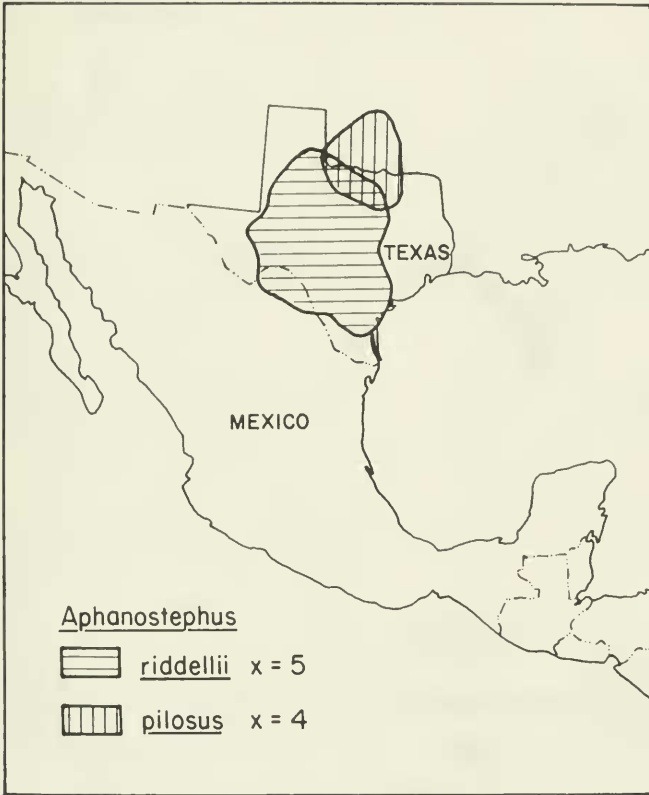


Fig. 3. Distribution of A. pilosus and A. riddellii.



Fig. 4. Distribution of varieties of *A. skirrhobasis*.

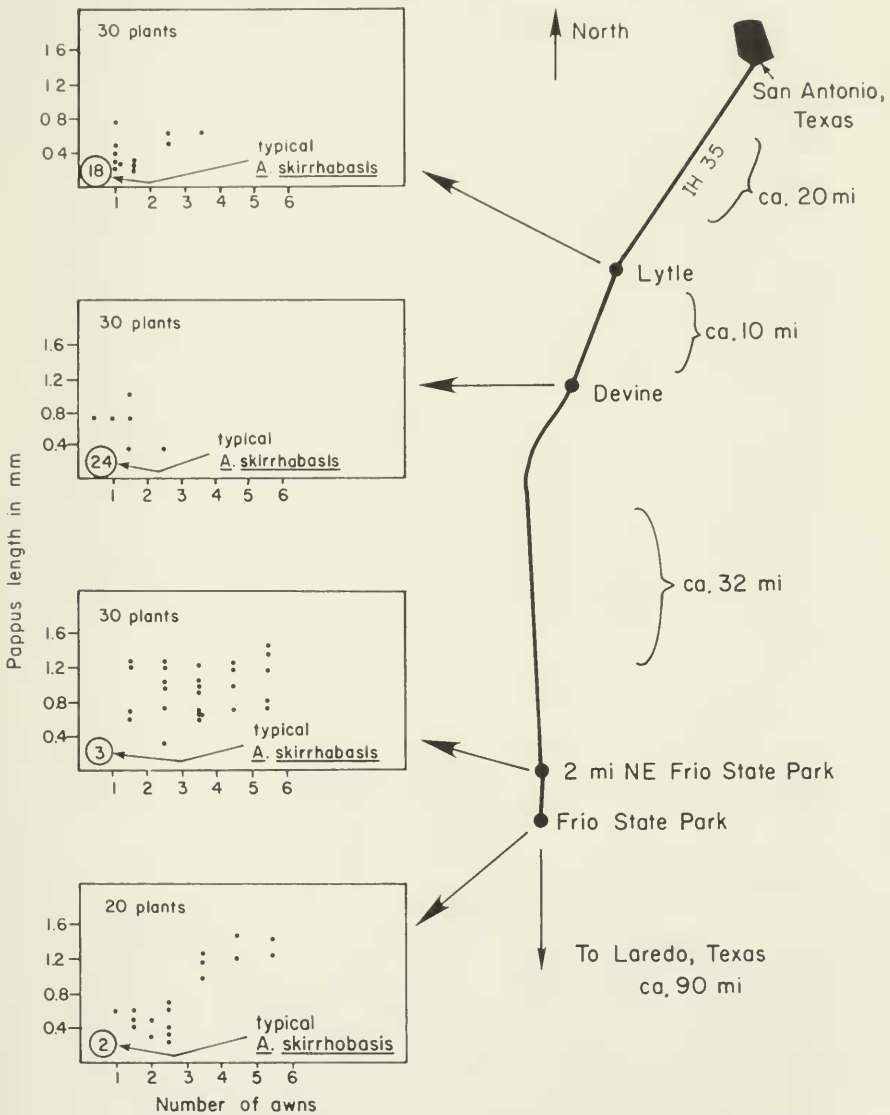


Fig. 5. Pappus variation in 4 populations of *Aphanostephus skirrhobasis*.